The Norway rat

Bennett G. Galef

Department of Psychology, Neuroscience & Behaviour

McMaster University

Hamilton, Ontario, Canada, L8S 4K1

Bennett G. Galef
Department of Psychology, Neuroscience & Behaviour
McMaster University
Hamilton, Ontario, Canada, L8S 4K1

Phone: (905) 525-9140, ext. 23017
Fax: (905) 529-6225
e-mail: galef@mcmaster.ca

Key words

aggression, audition, cognition, communication, development, domestication, food choice, learning, olfaction, reproduction, social learning, taste, thermoregulation, vision

Glossary

Circadian. Refers to rhythms of activity with a period of approximately 24 hr.

Conspecific. Used as either an adjective or noun to refer to another member of the same species, as contrasted with *heterospecific*, referring to a member of another species.

Dominance hierarchy. A linear or near linear ordering of the dominance relations of members of a group of animals.

Echolocation. The ability to use sound waves reflected from a surface to detect objects at a distance.

Ecology. The science concerned with the relationship between organisms and their environment.

Estrous cycle. The cycle of changes in the reproductive condition of female mammals.

Exotherm. An animal that depends on external sources of heat to maintain its body temperature in a viable range, as contrasted with *endotherms* that have physiological mechanisms to generate heat and reduce heat stress.

Fovea. A small are of the retina that provides great acuity.

Olfactor. Referring to the sense of smell.

Synopsis

Norway rats served for many decades as the main subject species in studies of animal behavior and its physiological and genetic substrates, and many tens of thousands of research papers were published concerning rats. Here, I first, discuss some of the reasons for the rise and fall of Norway rats as the focus of behavioral research with animals, then describe the origins of the domestic rat and natural history of its wild forebear before reviewing a few of the hundreds of areas of behavioral research in which Norway rats have served as subjects.

The Rise of Rats

Not all that many years ago, before the ethological approach to the study of animal behavior came to the fore early in the 1970s, comparative and physiological psychologists conducted most behavioral research with animals. The intent of these investigators was quite different from that of many of today's scientists with an interest in animal behavior. For the most part, comparative and physiological psychologists were interested in exploring general laws of behavior, particularly those laws governing the formation of the associations that underlie learning.

Because the focus of research was on discovery of general laws believed to be applicable to any species in any situation, convenience rather than theory or ecological considerations determined the choice of a species to study. And, one species proved more convenient than any other. Indeed, in the 1930s and 1940s, more than 60 percent of all papers published in two of the leading animal-behavior journals of the time (the *Journal of Comparative and Physiological Psychology* and the *Journal of Animal Behavior*) were concerned with the behavior of a single organism, the Norway rat (*Rattus norvegicus*).

Given the focus on discovery of general behavioral principles that might apply to all species, humans included, the Norway rat was not an altogether bad choice. Rats are members of the order Rodentia, the mammalian order with by far the greatest number of species (more than 2000), and of the genus *Rattus* (with more than 50 species), which is the most species rich of the murid family of rodents, the Muridae, that includes mice, gerbils and hamsters.

Rats are about average size for a mammal (reports of Norway rats as big as cats are considerable exaggerations; a very large adult male rat weighs 500 to 600 grams, making it a very small cat indeed) and a convenient size for laboratory work. Rats are neither so large as to

make their maintenance in large numbers impractical nor so small as to make direct observation of their behavior difficult or surgery on them particularly demanding. Domesticated rats are easy to produce. They become sexually mature at 3 months of age, have as a dozen or more pups in a litter, can produce a litter every 21 days and breed all year round. Further, the ability of rats to thrive on relatively low-protein diets makes them inexpensive to feed. Unlike their sometimes vicious and very timid, wild forebears, rats of domesticated strains are easy to handle and will go about their business undisturbed even when nearby humans are watching their every move.

Important advantages accrued from having, quite literally, hundreds of researchers working on various aspects of the behavior and physiology of a single species. Techniques developed, for example, in studies of rat learning were of use to scientists studying the rat nervous system, and studentsof learning in rats could benefit from information concerning rats' sensory systems. Further, the adequacy of the methods used in an experiment could be readily evaluated by others working with the same animal, so potentially important findings could be replicated (or not) almost immediately in a half-dozen laboratories.

The Fall of Rats

The decline in the dominance of Norway rats as subjects in behavioral research had a number of causes. Foremost among these was the mid-20th century increased interest in studying behavior among of a group of European biologists that called themselves ethologists. Ethological investigation of a species started with the construction of an ethogram, a complete description of the behavioral repertoire of a species when in its natural habitat.

Norway rats are, unfortunately, most active in the dark and underground, making them difficult to observe in the wild. Even worse, humans have inadvertently transported Norway rats

around the world making identification of their place of origin, their natural habitat, all but impossible. Today, most free-living Norway rats live in man-made structures, feed on human refuse or crops, and because of their close association with humans, are protected from many potential predators. Their current habitat is hardly natural.

Ethologists were particularly interested in interactions between animals and the environments in which they evolved. For example, the last of Tinbergen's four questions defining the field of ethology, and the question that was to serve as a focus of research in ethology's descendant field, behavioral ecology, concerned the functions of behavior (i.e. the ways in which behavior increased survival and reproductive success in natural circumstances). The behavior of Norway rats in their natural habitat, wherever it may be, is simple not available for such studies.

Ethologists focused their research not on individually learned behaviors but on instincts, species -typical patterns of behaviors that ethologists believed reflected directly the action of natural selection on the genetic substrate of behavior. One of the more appealing characteristics of rats to comparative psychologists was that rats did not seem to show elaborate, heritable, species-typical behaviors that could interfere with the discovery of general principles of behavior.

And, there were other problems as well. For example, the domesticated rats that were subject to so much attention from comparative psychologists had undergone several hundred generations of breeding in captivity. Exposure to artificial selection by humans breeding rats for tameness and for fertility in captivity ensured that the genetic substrate of domestic rats was not that of their wild forebears. A century or more of such artificial selection, led some ethologists

to assert that the behavior of laboratory rats was not `natural', and consequently, not worth studying.

As a practical matter, increasingly stringent regulations governing the breeding and maintenance of laboratory animals, made work with rats ever more expensive and reduced the number of laboratories that could afford to use rats in experiments. And invention of procedures for generating knockout strains of mice preceded the more-difficult development of knockout rat strains by 14 years. The importance of knockouts for exploring the genetic substrate of behavior made mice the species of choice for many scientists interested in studying mechanisms of mammalian behavior, even if using mice as subjects meant repeating behavioral studies previously performed with rats. In sum, although work on the behavior of Norway rats and its mechanistic substrate continues today, the dominant position of the species in studies of animal behavior is over.

What is the Origin of Laboratory Rats?

Norway rats, the forebears of all laboratory rat strains, are generally assumed to have originated somewhere in Asia, possibly in Northern China, although the long association of Norway rats with humans makes the species` point of origin difficult to determine. It is known that sometime in the mid-18th century, Norway rats spread through Europe (the appellation Norway rat is believed to derive from the false, 18th-century presumption that the first of the species arrived in the UK on lumber ships coming from Norway, although there were probably no *Rattus norvegicus* in Norway when the species first invaded Britain). The black or roof rat (*Rattus rattus*), not the Norway rat, was common in Europe before the larger and more aggressive Norway rat arrived in the 18th century and displaced them. Consequently, the black rat, not the Norway rat, was the principle vector in the recurring bouts of bubonic plague that

killed 25 percent or more of the human population of Europe during the latter half of the 14th century. Norway rats arrived on the east coast of North America shortly after their arrival in Europe, and spread with the gold rush to California in 1849. Today, Norway rats are to be found on every continent but Antarctica, and from Alaska (64° N) to South Georgia Island (55°S).

However, rats do not thrive in areas with continental climates, such as Alberta, Canada and northern Montana, USA, where winters are long and cold and human habitations are relatively sparse. Indeed, Norway rats are most successful in temperate climates. In the tropics, they are largely replaced by other species of their genus, for example, the more arboreal, lighter and longer-tailed *Rattus rattus* and *Rattus exulans* (the Polynesian rat).

Norway rats, like humans, are great generalists and are able to thrive in a broad range of environments. Rats have been seen catching fingerling trout in hatcheries, diving in rivers to feed on mollusks, and catching and killing wild ducks and geese. Wherever rats are introduced onto islands by human visitors (or when they swim or float to islands from distant shores), they become a threat to the survival of any ground-nesting birds found there and have been implicated in the extinction or endangerment of numerous bird species.

Norway rats are the forebears of all domesticated rat strains whether albino, hooded, black or agouti colored. When, where and how Norway rats were first domesticated is not known. In the 19th century, wild Norway rats served as prey in the brutal sport of rat baiting in which a dog was placed in a pit with large numbers of rats and bettors wagered on how many rats the dog would kill in a specified period. One story is that when rare albino wild Norway rats were trapped in the course of securing the large numbers of rats needed for rat baiting, the albinos were displayed in cages outside betting establishments, and that these albino rats were

the ancestors of at least some of today's domesticated strains. Whatever their source, domesticated albino rats were first used in the laboratory in 1895 at Clark University in Worcester, Massachusetts in studies of nutrition. Five years later, they were subjects in Willard Small`s studies, also at Clark, of the behavior of rats in mazes. The decades of subsequent research on the behavior of Norway rats and its neural substrate have led to publication of many tens of thousands of research articles. Obviously, it is not possible to thoroughly review so vast a literature here. Below, I describe a few of the many areas in which studies of Norway rats have played an important role, and mention a scattering of findings that I find either intriguing or amusing. A great deal more information concerning rats, both wild and domesticated, is available in the suggested readings.

Regulatory Systems

Some of the earliest studies of rat behavior were concerned with the role of behavior in maintaining the internal environment of animals within the boundaries compatible with life. The ability of rats to select items for ingestion, to regulate their intake so as to neither lose nor gain appreciable amounts of weight and to maintain a relatively constant body temperature each has an extensive literature.

<u>Selecting foods</u>

Results of experiments conducted in the 1940s and 1950s were interpreted by many as demonstrating that rats that had been deprived of a specific nutrient (for example, thiamine) could select the food containing thiamine from amongst a cafeteria of foods only one of which contained the needed vitamin. The results of these reports are responsible for the belief, widespread even today, that your body will lead you to seek out whatever foods you need to eat to remain healthy or to regain health should you become deficient in some nutrient.

Unfortunately, the interpretation of this early research has proven exaggerated. Although rats that need salt can identify salt in a food or fluid, and thirsty rats will seek water, rats fail miserably in selecting appropriate foods when in need of almost any other of the dozens substances (vitamins and minerals) needed for health.

Controlling body temperature

Like other mammals, rats use evaporative cooling to avoid heat stress. However, unlike humans and horses, rats do not sweat. Instead, overheated rats spread saliva on the unfurred areas of their bodies (as do elephants). The rat's naked tail (which some people find repulsive) serves as a particularly effective window through which to release heat. Consequently, rats that have had their tails surgically removed have a markedly reduced ability to remain cool when exposed to elevated environmental temperatures.

Reproductive Behavior

Every aspect of reproduction from selection of a mate to weaning of young has been studied in Norway rats. There are, for example, extensive and detailed studies of: (1) the cues that male rats use to determine if a female is in the receptive phase of her estrous cycle, (2) patterns of copulation and their effects on the rewards both male and female rats garner from engaging in sexual activity and the impregnation of females, (3) the behavior and sensory experiences of fetal rats and effects of intrauterine experiences on post-natal behavior (4) the nest building that females engage in before parturition, (5) behaviors during parturition when dams lick their pups, gather them in the nest and assume a nursing posture over them, (5) the behavior of young both while seeking their mothers nipples and nursing and when the mother is absent from the nest, (7) mother's behavior towards her maturing young: her retrieval of pups that stray from the nest, the gradual reduction in time she spends in contact with her offspring and changes

in maternal delivery of milk as her young mature, (8) the increased aggression of mothers with young, and (8) the changes in pups behavior as they develop from exothermic, blind, deaf and hairless eraser-sized newborns to independent juveniles.

Perhaps surprisingly, the seemingly helpless blind and hairless pups huddled together in a nest can behaviorally regulate their temperature, spreading apart and increasing the surface area of the huddle to increase heat loss when the environmental temperature is high and forming a tight ball with a small surface area when the environmental temperature is low. Equally surprising, is the impact of prenatal life on later behavior. As first discovered in Norway rats, whether a fetal mammal is located in its mother's uterus between two brothers or two sisters (i.e. its intrauterine position) profoundly influences the amount of testosterone to which it is exposed before birth. As was subsequently established in studies with mice and gerbils, much of an animal's hormonally influenced reproductive behavior when adult is modified by intrauterine exposure to testosterone.

Social Behavior

Free-living wild rats are intensely social beings that live in colonies consisting of from a few to several hundred individuals. Colony members share a burrow system and paths through the environment that they defend against intrusions by unfamiliar conspecifics.

Communication

Such social life requires communication, and Norway rats communicate in a variety of interesting ways. They produce olfactory cues that both allow individual identification and guide movement through the environment. They vocalize during social and sexual interactions and in response to the presence of potential predators, and much of their vocalization is ultrasonic (i.e. in a frequency range to high for humans to hear).

Aggression

Books have been written about the aggressive behavior of rats, describing the stimuli that elicit, direct and terminate aggressive interactions, the neural and endocrine substrates of aggression, and rats' postures and movements while interacting aggressively or stealing food from one another. Intruders into a the territory of a colony of wild rats are vigorously attacked, and even brief attacks on intruders that do not produce any detectable wounds can have fatal consequences, though the causes of such death are not well understood.

Predation

Laboratory rats' predatory behavior towards mice and the response of rats to cats and other potential predators were also studied for many years. However, ethical concerns have largely ended experiments involving either staged aggressive encounters between mammals or between predators and potential mammalian prey.

Social learning

Despite their aggressiveness towards strangers, members of established colonies of rats form stable dominance hierarchies and live relatively amicably, sleeping together, grooming one and following each other through the environment. Life in socially tolerant groups provides rats with opportunities to both observe and learn from the behavior of others of their species. More than 50 papers have been published concerned with the finding that after a naïve "observer" rat interacts for a few minutes with a "demonstrator" rat that has recently eaten a distinctively flavored food, the observer rat shows a substantial increase in its liking for whatever food its demonstrator ate.

Rats have also been shown to learn to dig for buried food by watching other rats do so. After learning socially either to eat a particular food or to dig for food, an observer rat can act as

a demonstrator for new, naïve observers, and such chaining can be sustained for several "generations" thus producing rat "traditions."

Sensory systems

Rats are sensitive to a broad range of stimuli; they see, hear, taste, smell, and respond to touch. Each of the rat's sensory system has been fully explored, and each has its own voluminous literature.

Vision

In nature Norway rats are most active at dusk and dawn, and possibly as a result, they are less dependent on vision than other well-studied mammals such as cats and ferrets. The visual, acuity, even of wild rats is quite poor, and domesticated rats have about half the visual acuity of their wild brethren with albino strains of rat suffering from particularly poor vision. All strains of Norway rat lack both color vision and a fovea, and their visual cortex is less clearly functionally differentiated than that of some other mammals.

Olfaction

Rats have a keen sense of smell and, throughout life, depend heavily on olfactory cues in their day-to-day functioning. Prenatal exposure to odorants can have lasting effects on rats postnatal behavior. Infants quickly learn to identify the odor of their mother and home nest and use olfactory cues to find their mother's nipples to nurse. Adult rats deposit scent marks in the environment that allow others to identify their age, sex, reproductive state and dominance status. Most impressive, the reproductive behavior of female rats can be markedly affected by olfactory cues; exposure to strange males both accelerates the age of onset of puberty and the regularity and timing of estrous cycles.

Taste

The taste perceptions of rats and humans are surprisingly similar. Members of the two phylogenetically quite distant mammals almost always find the same flavors attractive or repulsive. Consequently, Norway rats have served as models for understanding human taste perception. Like humans, rats display different facial expressions when experiencing pleasant and unpleasant flavors. However, there is no evidence that the disgust faces of rats dissuade other rats from eating the food that a grimacing animal has found distasteful. Also like humans, rats find it particularly easy to associate experience of an unfamiliar flavor, but not an unfamiliar noise or visual cue, with later gastrointestinal upset. After a single experience, both rats and humans learn to avoid a novel flavor to which they were exposed hours before becoming ill.

Hearing

Relative to humans, hearing in rats is shifted towards higher frequencies, and rats can detect sounds with frequencies as high as 80 kHz. Rats produce a number of auditory signals both audible to humans and in the ultrasonic range. Relatively little work has been done on audible rat vocalizations, possibly because of their great variability. However, rats' more stereotyped ultrasonic vocalizations and the responses to them have received considerable attention.

Ultrasonic calls (40-50 kHz) are emitted by infant rats when they cool. Adult rats emit a 22 kHz `long-call` in aversive situations (for example, after losing a fight or detecting a cat) and, perhaps surprisingly, after ejaculating. Rats also emit a 50 kHz `chirp' that may be associated with pleasant events (for example, playing or being tickled) that has been described as a form of laughter, although it also occurs in some unpleasant circumstances, for example, during aggression or in response to some types of pain.

All these ultrasonic vocalizations can affect the behavior of rats that hear them. Mother rats are attracted to the ultrasonic vocalizations of pups, and there is some evidence that exposure to 22 kHz long calls increases the wariness of rats hearing them. Although rats can use their ultrasonic vocalizations to detect objects at a distance, they are far less sophisticated in their use of ultrasound for echolocation than are bats.

Somatosensation

The sense of touch plays in important role in rats' movements about their environment. Rats are "thigmotactic," they are biased towards remaining in physical contact with vertical surfaces, presumably to protect against predation. Rats' vibrissae, the whiskers around their noses, are extremely sensitive to tactile stimuli, and have been compared with human fingertips. Rats can move their vibrissae independently across surfaces allowing them to discriminate among objects of different size, texture and shape.

Learning & Cognition

In the decades when rats were the predominant species in behavioral studies, they most often served as subjects in investigations of learning. At first, such studies took place in complex mazes with many choice points that were believed to mirror the complex burrow systems in which wild rats live. When behavior in such complex environments proved intractable to analysis, experimenters shifted to simple T-mazes with only a single choice point. Finally, rats were studied in highly automated Skinner boxes, where subjects were rewarded for pressing levers with food delivered on various schedules.

Most recently, studies of the ability of rats to solve cognitively demanding tasks have been in vogue. In the Morris water maze, rats are placed, on successive trials, in random locations in a small circular tank filled with water. To escape from the water, which the rats find

mildly aversive, they have to learn the location of a platform hidden just beneath the water's surface. In different version of the task, the rats can use visual cues in the surrounding room, a beacon directly indicating the location of the platform, or information concerning the distance of the platform from the wall of the test chamber to find it. Solution of the task using cues outside the pool itself can require the rat to form a `cognitive map` of the relationship between cues in the room and the location of the platform.

Perhaps the most challenging task with which rats have been presented is the multi-arm maze. Here, as the name of the apparatus implies, a rat is placed on the central platform of a maze with several arms (eight is the most common number) and a small piece of food is placed at the end of each arm farthest from the central platform. The rat is free to explore the maze until it has recovered food from the end of each arm. Greatest efficiency requires that a rat enter each arm of the maze only once, a performance that requires the subject to remember which arms it has previously entered. Rats are extraordinarily good at this task, and make relatively few errors, rarely reentering a previously visited arm of the maze.

Conclusion

In this brief article I have just begun to scratch the surface of research on the behavior of rats. Many topics that have been the focus of extensive research have not even been mentioned, among them: play, circadian rhythms in activity, motivation, schedules of reinforcement, memory, the results of domestication, maternal effects on development, postures, locomotion, grooming, exploratory behavior, response to pain, or rats as model systems to study human behavioral disorders such as anxiety or obsessive-compulsive disorder. This list could be lengthened considerably without difficulty.

The further readings listed below provide both greater depth and greater breadth of coverage of the role of rats in both science and everyday life than this brief article. Barnett`s *The Rat: a Study in Behavior,* although it is somewhat dated, provides classic descriptions of the behavioral repertoires of wild rats and discussion of some laboratory work with domesticated rats,. Meehan`s *Rats and Mice: Their Biology and Control* provides an introduction to the extensive literature on the control of pest populations of rats. Both Telle's and Calhoun's classic articles are difficult to find today, but provide some of the best descriptions available of the social behavior of wild rats. Munn's *Handbook of Psychological Research on the Rat* provides a summary of research with laboratory rats in its heyday. Other recommendations provide introductions to specific topics covered here. Most important among these is Wishaw and Kolb`s recent, 500-page edited volume *The Behavior of the Laboratory Rat*. It provides a compact and up-to date-summary of much of the work on domesticated rats.

Several publications about Norway rats intended for lay audiences have appeared during the last decade. S. A. Barnett's "*The Story of Rats*" and Lore & Flannelly's "*Rat societies*" are both trustworthy.

Further Readings:

Barnett S A (1975) *The Rat: A Study in Behavior*. Chicago: University of Chicago Press.

Barnett SA (2001) *The Story of Rats*. Crow's Nest, New South Wales: Allen & Unwin

Burn CC (2008) What is it like to be a rat? Sensory perception and its implications for experimental design and rat welfare. *Applied Animal Behaviour Science* 122: 1-32.

Calhoun JB (1963) *The Ecology and Sociology of the Norway Rat*. Public Health Service Publication no. 1008. Bethesda, Maryland: U.S. Department of Health.

Galef BG Jr (1991) A contrarian view of the wisdom of the body as it relates to food selection *Psychological Review* 98: 218-224.

Lore R and Flannelly K (1977) Rat societies. *Scientific American* 236: 106-115.

Meehan AP (1984) *Rats and Mice: Their Biology and Control*. East Grinstead, UK: Rentokil Ltd.

Munn NL (ed.) (1950) *Handbook of Psychological Research on the Rat: an Introduction to Animal Psychology*. Cambridge, Massachusetts: Riverside Press.

Shair HN Barr GA and Hofer MA (eds.) (1991) *Developmental Psychobiology: New Methods and Changing Concepts*. Oxford: Oxford University Press.

Shettleworth SJ (1998) *Cognition, Evolution and Behavior*. Oxford: Oxford University Press.

Stricker EM (ed.) (1990) *Neurobiology of Food and Fluid Intake*. New York: Plenum Press.

Telle HJ (1966) Beitrag zur Kenntnis der Verhaltensweise von Ratten, vergleichend dargestellt bei Rattus rattus und Rattus norvegicus. *Zeitschrift fur Angewandte Zoologie* 53: 129-196.

Whishaw I Q & Kolb B (eds.) (2005) *The Behavior of the Laboratory Rat: A Handbook with Tests*: Oxford: Oxford University Press.